THE ROYAL SOCIETY

Kin recognition and the 'armpit effect': evidence of self-referent phenotype matching

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In species with multiple paternity or maternity, animals may best assess their relatedness to unfamiliar conspecifics by comparing their own phenotype(s) with those of unidentified individuals. Yet whether animals can recognize kin through self-matching is controversial. Because golden hamsters (*Mesocricetus auratus*) mate multiply and can produce multiply sired litters, they were tested for their ability to use self-matching for kin recognition. Hamsters that were reared only with non-kin since birth responded differentially to odours of unfamiliar relatives and non-relatives. Postnatal association with kin was not necessary for this discrimination. Prenatal learning was unlikely because of delayed production and perception of social odours. To our knowledge, this is the first demonstration that a vertebrate can use its own phenotype for kin-recognition purposes without prior experience with kin. By using itself as a referent, rather than its siblings or parents, a golden hamster may be better able to direct nepotism towards the most appropriate individuals. Kin discrimination via self-inspection may be especially important in nepotistic contexts (to identify most closely related conspecifics), whereas inclusion of the phenotypes of close kin as referents may be favoured in mate-choice contexts (to identify all related individuals).

Keywords: kin discrimination; development; nepotism; mate choice; olfactory behaviour; hamster

1. INTRODUCTION

Many vertebrates and invertebrates appear to recognize unfamiliar relatives or can discriminate among equally familiar kin based on degrees of relatedness (e.g. Fletcher & Michener 1987; Hepper 1991; Sherman *et al*. 1997). This ability is usually attributed to a phenotype-matching mechanism (Holmes & Sherman 1982), in which an individual learns its own phenotype(s) and/or those of its familiar kin, stores a representation of these traits in memory (a 'kin template'), and later compares or matches the phenotypes of unidentified animals to this template (see also Sherman *et al*. 1997). Phenotype matching requires a correlation between phenotypic similarity and genotypic similarity, so that individuals with traits that most closely match an animal's template are its closest kin.

Self-referent phenotype matching, the ability of animals to learn and use their own phenotypes as referents for recognition of relatives (dubbed the 'armpit effect' by Dawkins (1982)), enables the most accurate assessment of the degree of relatedness between two individuals because one's own cues will generally reflect one's own genotype more accurately than cues of close kin. Self-matching should be favoured in species with multiple paternity or maternity or when individuals commonly encounter older (or younger) siblings after dispersal (Holmes 1986; Holmes & Sherman 1982; Sherman 1991). This mechanism may mediate nepotistic behaviours (dispensing benefits only to kin; Holmes & Sherman 1982; Sherman *et al*. 1997), mate-choice decisions (optimizing the costs and benefits of inbreeding and outbreeding; Alexander 1991; Sherman *et al*. 1997) or both (see also Lenington 1991; Ober *et al*. 1999; Wedekind *et al*. 1995).

The likelihood of a self-matching mechanism in nepotistic (compared with mating) contexts is controversial. Alexander (1990, 1991) argued against the evolution of self-matching in nepotism because alleles underlying such recognition would be 'genetic outlaws', benefiting themselves at a cost to the remainder of the genome, and thus would be suppressed by unlinked alleles not involved in the recognition process. Others (Dawkins 1982; Hamilton 1987; Sherman 1991; Sherman *et al*. 1997) have countered that if alleles involved in both generating and perceiving recognition cues are spread throughout the genome, then all alleles, including those not involved in recognition, would benefit from 'recognizing' corresponding alleles in conspecifics. Indeed, self-matching may be favoured in nepotistic situations, in which animals need to identify individuals to whom they are most closely related (e.g. Getz & Smith 1986; Grosberg & Quinn 1986; Manning *et al*. 1992; Petrie *et al*. 1999). In contrast, additional referents (such as parents and siblings) should be used in mate-choice decisions, to help animals identify all individuals to whom they are closely related (e.g. Penn & Potts 1998; Simmons 1989).

Self-referent phenotype matching in nepotistic contexts has also been questioned on empirical grounds. Although there is suggestive evidence of self-matching in honeybees and Belding's ground squirrels (Getz & Smith 1986; Holmes 1986), Alexander (1990, 1991) claimed that these data could be explained as social-learning errors, with animals mistaking unfamiliar relatives for familiar ones and thus appearing to be able to recognize unfamiliar kin without prior association. To date, no study implicating self-matching has eliminated all possible sources of social learning about relatives. We used an experimental design that had several improvements over previous studies to

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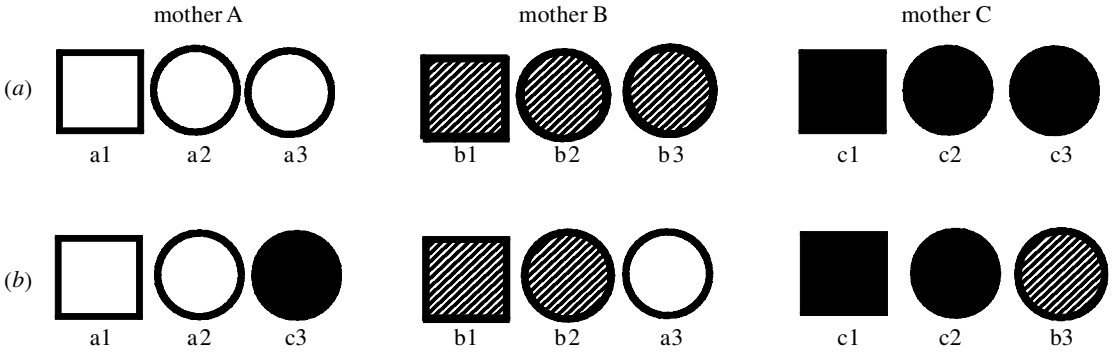

Figure 1. Schematic of the cross-fostering paradigm. (*a*) Litters on day of birth; (*b*) litters after cross-fostering. Within 12 h of birth, litters were reduced to one male (squares) and two female (circles) pups. One female pup was transferred to a second litter, and one female pup from a third litter took her place in the first litter. After weaning, cross-fostered females (e.g. female c3) were tested for their responses to flank-gland odours from a familiar unrelated male (NSRT, e.g. a1), an unfamiliar brother (SRA, e.g. c1) and an unfamiliar unrelated male (NSRA, e.g. b1). They were also tested with females' odours from the same classes of familiarity relatedness (e.g. NSRT, a2; SRA, c2; NSRA, b2). Shading denotes relatedness.

assess the ability of adult golden hamsters (*Mesocricetus auratus*) to recognize unfamiliar kin without early exposure to traits of their siblings or mother.

Golden hamsters are nocturnal, burrowing rodents that inhabit arid regions of Syria. They live solitarily and defend their food caches and burrow systems against most conspecifics. Field reports suggest home ranges of 2000 m^2, with ranges of males and females overlapping (Murphy 1977). Captive females will mate with several males and produce litters with multiple paternity (Huck *et al*. 1985, 1986), a situation favouring a self-matching mechanism (e.g. Sherman 1991). Olfactory signals are the predominant means of communication and recognition in *M. auratus*, involving an array of glands that are sexually dimorphic and individually distinct (Johnston 1990; Johnston *et al*. 1993). In captivity, odours from flank glands vary with relatedness, as siblings' odours are treated as more similar than those of non-siblings (Todrank *et al*. 1998). Additionally, captive hamsters discriminate between the flank-gland odours of unfamiliar kin and non-kin (Heth *et al*. 1998), suggesting the possibility that they can use a self-referent phenotype-matching mechanism.

We used several responses to odours as assays for recognition, including investigation time and two scent-marking behaviours. Flank marking (the flank gland rubbed along a surface) is an agonistic response to conspecifics or their odours and may function in intrasexual competition, territory defence and mate choice. Vaginal marking by females (the ano-genital region pressed on the substrate while walking) functions primarily for sexual advertisement, since it is preferentially directed at males and peaks in frequency the day before sexual receptivity (Johnston 1977, 1990). Both marking behaviours are more frequent towards unfamiliar non-kin than towards familiar kin (Heth *et al*. 1998).

We examined the responses of cross-fostered females, reared without exposure to kin, to odours of related and unrelated individuals. If hamsters can use self-referent phenotype matching to assess their relatedness to unfamiliar individuals (i.e. using their own odours), then females should perceive odours of unfamiliar non-kin as novel compared with their own odours, whereas odours of unfamiliar kin should be perceived as similar to their own odours. Further, if self-referent matching evolved for fine-tuned discrimination abilities, we would expect hamsters' own odours to be weighted more heavily in their kin templates than odours of their rearing associates (mother and siblings). We thus predicted that females would discriminate between an unfamiliar relative's odour and that of an unfamiliar relative of their foster siblings.

2. METHODS

(a) *Housing*

Animals were housed in solid-bottom polycarbonate cages (38 cm × 30 cm × 17 cm) with Sani-chip bedding and *ad libitum* food (Prolab 1000 Agway, Ithaca, NY, USA) and water. Mothers were provided with cotton batting for nesting three days prior to parturition. The colony was maintained on a reversed 14 L:10 D schedule at 21 ± 1 °C and 50% relative humidity. About 90% of the subjects' grandparents were laboratory stock derived from Charles River random-bred animals, with the remainder purchased from Charles River Laboratories (Wilmington, MA, USA).

(b) *Cross-fostering procedure*

Eighteen female pups were cross-fostered immediately after birth (figure 1). Specifically, after a litter was reduced to one male and two female pups, one of these females (arbitrarily chosen) was transferred to a newly parturient foster mother; a female pup from a third family was then added to the litter. Thus each mother reared one biological son and daughter and one foster daughter. Latex gloves were worn when handling pups. Because parturition lasts 1–3 h and there is considerable variation in the timing of births, pups were 3–12 h old (mean 6.0 ± 0.6 h) when transferred. Young were separated from the mother and housed singly at 30 days of age; weaning occurs around 21 days of age. Thus cross-fostered females were never exposed to kin phenotypes other than their own after fostering.

(c) *Testing procedure*

Between 41 and 61 days of age, the sexually mature, cross-fostered females (hereafter, 'females') were tested for their responses to flank-gland odours from unfamiliar kin and non-kin of both sexes. The flank glands of a 'donor' animal were rubbed back and forth (about 12 times) against a 7.6 cm × 17.8 cm glass plate at two locations *ca.* 2 cm apart. The plate

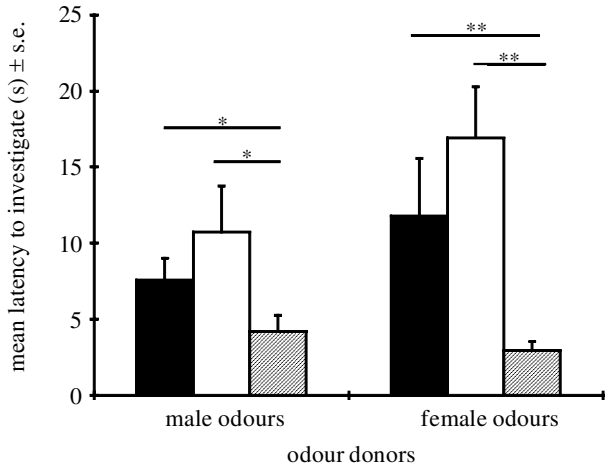

Figure 2. Mean latency (s ± s.e.) to investigate flank-gland odours during 5 min discrimination tests. Cross-fostered females were presented with odours from familiar non-kin (filled bars, non-siblings reared together (NSRT)), unfamiliar kin (open bars, siblings reared apart (SRA)) and unfamiliar non-kin (hatched bars, same-aged non-siblings reared apart (NSRA); see § 2(d) for sample sizes). Horizontal lines denote significant ($^{*}p < 0.05$, $^{**}p \leqslant 0.01$) differences in responses to two odours, based on repeated-measures ANOVAs.

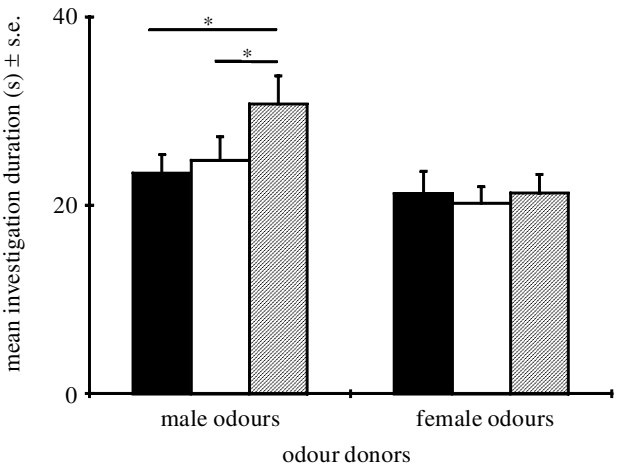

Figure 3. Mean duration of investigation (s ± s.e.) of flank-gland odours during 5 min discrimination tests. Cross-fostered females were presented with odours from familiar non-kin (filled bars, non-siblings reared together (NSRT)), unfamiliar kin (open bars, siblings reared apart (SRA)) and unfamiliar non-kin (hatched bars, same-aged non-siblings reared apart (NSRA); see § 2(d) for sample sizes). Horizontal lines denote significant ($p < 0.05$) differences in responses to two odours, based on a repeated-measures ANOVA.

was placed in one end of a female's cage for a 5 min test trial. Odours were collected and coded by someone other than the observer ⩽10 min before presentation. Latex gloves were worn while handling plates to reduce transfer of human or other hamster odours to the plates. After use, plates were washed with PEX laboratory glassware cleaner, rinsed in hot water, and allowed to air-dry.

Females were tested on their pro-oestrous days (the dark period 12–24 h before sexual receptivity, as determined by brief pairings with an unfamiliar, unrelated male), because rates of female scent marking are highest on this day (Johnston 1977). Tests were conducted in a separate, dimly lit room between 09.00 and 15.00. Females were presented with two odours on each test day (for a total of four test days over a 22-day period), and were returned to the colony room for 1–3 h between tests on a given day. During each 5 min test, the latency and duration of investigation of odours (nose within 0.5 cm) were measured with a stopwatch. The numbers of flank and vaginal marks were also recorded. All data collection was blind with regard to the identity of odour donors.

(d) *Odours used during tests*

Females were tested with male and female odours of three categories presented in a counterbalanced order (see figure 1): non-siblings reared together with the female (NSRT, familiar but genetically unrelated; 17 females tested with male odours and 13 with female odours), full siblings reared apart (SRA, unfamiliar but genetically related; 17 females tested with male odours and 14 with female odours), and same-aged non-siblings reared apart (NSRA, unfamiliar and genetically unrelated; 18 females tested with male odours and 18 with female odours). After log transformation, each dependent variable was analysed with a repeated-measures ANOVA (NSRT × SRA × NSRA), separately for male and female odours. General linear contrasts (CMATRIX command in Systat) were used to examine differences between relatedness–familiarity groups within each sex. To assess relative weighting of odours in kin templates, on the final testing day nine subjects were presented with flank-gland odour from their unfamiliar biological sister and from the unfamiliar sister of their foster siblings (e.g. female c3 presented with odours from females c2 and a3; figure 1) simultaneously for 5 min. Data are presented as non-transformed means ± s.e.

3. RESULTS

(a) *Latency to investigate odours*

Female hamsters approached male flank-gland odours differentially ($F_{2,30} = 4.83$, $p = 0.02$; figure 2, left-hand side). The latency to investigate the odours of male-NSRA was shorter than for odours of male-SRA ($p = 0.01$) or male-NSRT ($p = 0.04$). Females showed the same pattern of response to the odours of other females ($F_{2,16} = 7.70$, $p = 0.005$; figure 2, right-hand side). Subjects approached and investigated female odours of NSRA more quickly than odours of either SRA ($p = 0.006$) or NSRT ($p = 0.03$).

(b) *Duration of odour investigation*

Duration of investigation of male flank-gland odours varied with relatedness and familiarity ($F_{2,30} = 3.15$, $p = 0.05$; figure 3, left-hand side). Females spent significantly more time investigating odours from male-NSRA than those from male-SRA ($p = 0.04$) or male-NSRT ($p = 0.05$). There were no significant differences in duration of investigation of female odours.

(c) *Scent-marking behaviours*

Odours of males elicited differential levels of flank marking by females ($F_{2,30} = 3.65$, $p = 0.04$; figure 4, left-hand side): they marked less in response to odours from NSRA than SRA ($p = 0.045$) or NSRT ($p = 0.03$). There were no significant differences in the frequency of vaginal

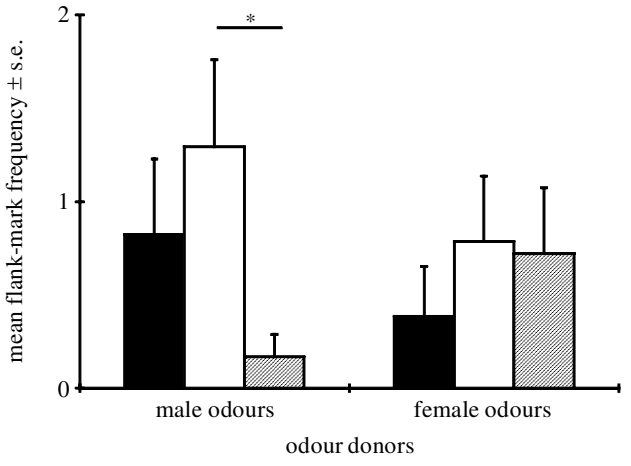

Figure 4. Mean frequency (± s.e.) of flank marking by females following presentation of odours during 5 min discrimination tests. Females were presented with flank-gland odours from familiar non-kin (filled bars, non-siblings reared together (NSRT)), unfamiliar kin (open bars, siblings reared apart (SRA)) and unfamiliar non-kin (hatched bars, same-aged non-siblings reared apart (NSRA); see § 2(d) for sample sizes). The horizontal line denotes significant ($p < 0.05$) difference in responses to odours, based on a repeated-measures ANOVA.

marking in response to odours from different male or female donors.

In summary, females were attracted to and preferred odours of unfamiliar non-kin over odours of unfamiliar kin. In addition, females rarely flank marked in response to male-NSRAs' odours. We interpret these behaviours as suggestive of a mating preference for unrelated, unfamiliar males and an avoidance of familiar or related males, since we tested females on the day of their reproductive cycle when they typically exhibit mate-choice behaviours (Huck *et al*. 1986).

(d) *Relative weighting of odours in kin template*

Subjects investigated odours from their unfamiliar biological sisters longer than those from the unfamiliar sisters of their foster siblings (mean duration of investigation ± s.e. = 8.37 ± 1.86 s and 5.60 ± 0.97 s, respectively; two-tailed paired *t*-test: $t_8 = 2.44$, $p = 0.04$). Thus females' own odours were apparently weighted more heavily in their templates than those of their foster family.

4. DISCUSSION

Cross-fostered female *M. auratus* behaved differentially toward odours of unfamiliar related and unrelated hamsters, investigating odours of unfamiliar non-kin sooner and for longer than odours of unfamiliar kin (SRA and NSRA; figures 2–4). At first glance, female odours appear to have been less discriminable than male odours. However, the latency data indicate that subjects identified both female and male odours before approaching (consistently investigating NSRA odours more quickly than SRA or NSRT odours; figure 2), and therefore it was not necessary for hamsters to continue investigating odours in an effort to classify them. Thus subjects perceived differences among female odours, but for whatever reason were not 'motivated' to act differentially upon these odours (e.g. by scent marking). We conclude from our results that recognition of unfamiliar kin by hamsters was mediated by a self-referent phenotype-matching mechanism (females used their own odours as referents for comparison with unidentified odours), because females had no opportunity to learn kin odours from other sources (see below). Captive hamsters are inbred (Murphy 1985), so their odours are probably less variable than those of outbred wild hamsters. That captive hamsters can still identify unfamiliar kin despite inbreeding suggests that recognition through self-matching may be a robust, widespread phenomenon.

Our data do not eliminate the possibility that females learned the odours of their biological siblings *in utero* or during the first few hours after birth. However, early learning is unlikely for several reasons. First, females that spent more time with their biological mother and siblings prior to cross-fostering were no more discriminating than females that were fostered immediately after birth. Neither the latency nor the duration of investigation by females of any of the six odours was significantly correlated with the number of hours each female spent in her natal nest prior to fostering (Spearman's rank-order correlations, n-values = 13–18; all $p > 0.10$). Second, *M. auratus* flank glands do not begin secreting until one month after birth (Algard *et al*. 1966), thus precluding prenatal or early postnatal learning of this odour. Learning of other complex odours (e.g. maternal cues in amniotic fluid; e.g. Hepper 1987) prior to transfer is unlikely also, because few neural projections from the olfactory bulb to the rest of the brain are present at birth (Leonard 1975; gestation is only 16 days) and because pups do not respond preferentially to species-specific odours until eight days after birth (Devor & Schneider 1974). Third, in contrast to rapid development of mother–offspring recognition in precocial species (e.g. Gubernick 1981), learning of kin cues generally develops later or more slowly in non-communal, altricial species, in which immobile young are confined to a nest during early development and there is no selective benefit to developing recognition abilities before they are needed and no cost to delaying learning (see also Holmes & Sherman 1982). Mechanistically, learning of siblings' cues is not likely to be dependent on the prenatal period when the odours of individuals change after birth and during development (e.g. around weaning; J. M. Mateo, unpublished data). Thus rapid or one-trial learning of siblings' cues is not likely to be an adaptive strategy for non-communal altricial species (cf. Alexander 1991).

In contrast to females' discrimination of odours of unfamiliar siblings (SRA) and unfamiliar non-kin (NSRA), subjects responded similarly to odours of SRA and familiar non-kin (NSRT), demonstrating that the traits of unrelated foster siblings were also incorporated into females' templates for kin phenotypes. Thus, as in Belding's ground squirrels (Holmes & Sherman 1982), golden hamsters have at least two mechanisms for kin recognition: familiarity (established during early rearing) and self-referent phenotype matching. Different kin-recognition mechanisms may be used in different contexts, such as mate choice and nepotism, depending on the ecology and sociality of the species (Holmes & Sherman 1982; Sherman 1991; Sherman *et al*. 1997).

Our data suggest that a female's own odours were weighted more heavily in her kin template than odours of early rearing associates (foster siblings and mother), suggesting that there may be a special mechanism for attending to one's own traits or for weighting them more when comparing phenotypes. For example, during early development an animal's olfactory epithelium may become more 'tuned' to its particular mix of odours, thereby increasing the salience of those odours later in development (e.g. Leon *et al*. 1987). In addition, females' own odours may acquire salience because they are exposed to their own odours almost continually and at high concentrations, even if other individuals are present in a nest. After dispersal from the natal nest an individual's odours could obtain even greater weight or salience if the individual lives alone.

Given the spatial distribution of free-living *M. auratus*, with ranges of several males overlapping with a female's range (Murphy 1977) and the occurrence of mixed-paternity litters in the laboratory (Huck *et al*. 1985, 1986), a self-referent matching mechanism may allow hamsters to discriminate among close kin, such as maternal full- and half siblings, or to recognize paternal half siblings. This recognition, and the behaviours that result (e.g. differential agonism toward kin and non-kin), may be used by hamsters to facilitate nepotism, such as burrow sharing and access to food caches after natal dispersal or during periods of high population densities (Murphy 1977). Consistent with this hypothesis, female hamsters living in a semi-natural arena spend significantly more time near their full sisters and are less agonistic toward them than non-sisters (despite having been separated from their sisters for up to seven months), as would be predicted if kin recognition functioned in nepotistic contexts. In contrast, captive females are equally likely to exhibit lordosis to and mate with full brothers and non-brothers, which would not be expected if kin recognition evolved for mate choice (J. M. Mateo and R. E. Johnston, unpublished data). Regardless of the ultimate function of hamster kin recognition, our results provide the first clear evidence for a self-matching mechanism in vertebrates, despite over 30 years of kin-recognition research.

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